

ASSEMBLAGE ORGANIZATION IN STREAM FISHES: EFFECTS OF ENVIRONMENTAL VARIATION AND INTERSPECIFIC INTERACTIONS

GARY D. GROSSMAN, ROBERT E. RATAJCZAK, JR., MAURICE CRAWFORD,¹ AND MARY C. FREEMAN²

Daniel B. Warnell School of Forest Resources, University of Georgia, Athens, Georgia 30602 USA

Abstract. We assessed the relative importance of environmental variation, interspecific competition for space, and predator abundance on assemblage structure and microhabitat use in a stream fish assemblage inhabiting Coweeta Creek, North Carolina, USA. Our study encompassed a 10-yr time span (1983–1992) and included some of the highest and lowest flows in the last 58 years. We collected 16 seasonal samples which included data on: (1) habitat availability (total and microhabitat) and microhabitat diversity, (2) assemblage structure (i.e., the number and abundances of species comprising a subset of the community), and (3) microhabitat use and overlap. We classified habitat availability data on the basis of year, season, and hydrologic period. Hydrologic period (i.e., pre-drought [PR], drought [D], and post-drought [PO]) represented the temporal location of a sample with respect to a four-year drought that occurred during the study. Hydrologic period explained a greater amount of variance in habitat availability data than either season or year. Total habitat availability was significantly greater during PO than in PR or D, although microhabitat diversity did not differ among either seasons or hydrologic periods. There were significantly fewer high-flow events (i.e., $\geq 2.1 \text{ m}^3/\text{s}$) during D than in either PR or PO periods. We observed a total of 16 species during our investigation, and the total number of species was significantly higher in D than in PR samples. Correlation analyses between the number of species present (total and abundant species) and environmental data yielded limited results, although the total number of species was inversely correlated with total habitat availability. A cluster analysis grouped assemblage structure samples by hydrologic period rather than season or year, supporting the contention that variation in annual flow had a strong impact on this assemblage. The drought had little effect on the numerical abundance of benthic species in this assemblage; however, a majority of water-column species increased in abundance. The increased abundances of water-column species may have been related to the decrease in high-flow events observed during the drought. Such high-flow events are known to cause mortality in stream fishes. Microhabitat use data showed that species belonged to one of three microhabitat guilds: benthic, lower water column, and mid water column. In general, species within the same guild did not exhibit statistically distinguishable patterns of microhabitat use, and most significant differences occurred between members of different guilds. However, lower water-column guild species frequently were not separable from all members of either benthic or mid-water-column species. Variations in the abundance of potential competitors or predators did not produce strong shifts in microhabitat use by assemblage members. Predators were present in the site in only 9 of 16 seasonal samples and never were abundant (maximum number observed per day was 2). In conclusion, our results demonstrate that variability in both mean and peak flows had a much stronger effect on the structure and use of spatial resources within this assemblage than either interspecific competition for space or predation. Consequently, we suspect that the patterns in both assemblage structure and resource use displayed by fishes in Coweeta Creek arose from the interaction between environmental variation and species-specific evolutionary constraints on behavior, morphology, and physiology.

Key words: community organization; droughts; floods; interspecific competition; microhabitat use; predation; resource partitioning; spatial resources.

INTRODUCTION

The structural and functional properties of ecological assemblages may be determined through a variety of

mechanisms. The three most common organizational mechanisms appear to be resource limitation, environmental variability, and predation (Connell 1978, Grossman et al. 1982, Menge and Sutherland 1987). In habitats where resource limitation is a frequent occurrence, assemblage structure (i.e., the number and abundances of species comprising a subset of the community) and resource use are primarily driven by changes in resource availability coupled with the differential competitive abilities of assemblage members (Grossman et al. 1982, Menge and Sutherland 1987, Gotelli and

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¹ Present address: Department of Zoology, North Carolina State University, Box 7617, Raleigh, North Carolina 27695-7617 USA.

² Present address: U.S. Geological Survey, Biological Resources Division, Patuxent Wildlife Research Center, Warnell School of Forest Resources, University of Georgia, Athens, Georgia 30602 USA.

Graves 1996). Assemblage structure in these systems tends to be relatively stable or correlated with changes in resource availability (Grossman et al. 1982), and species minimize the deleterious effects of interspecific competition by minimizing overlap on limiting resources. Conversely, the structure and resource use patterns of assemblages commonly subjected to intense and unpredictable environmental fluctuations are predominantly determined by the interaction between a given disturbance and species-specific evolutionary constraints on behavior, morphology, and physiology (McIntosh 1995). Assemblage structure may vary substantially in these systems, and species commonly exhibit considerable overlap in resource use. Coexistence with high resource overlap is possible within these assemblages, because environmental variation is sufficiently intense to reduce species abundances to levels below which resource limitation occurs, or shifts competitive advantages from one species to another (Grossman et al. 1982, Pickett and White 1985, McIntosh 1995). Finally in predator mediated systems, assemblage structure and patterns of resource use vary in concert with predator abundance (Paine 1966, Menge and Sutherland 1987). Typically, species richness and resource overlap are higher when predators are present, because they preferentially prey on dominant competitors who would otherwise exclude inferior competitors (Paine 1966, Menge and Sutherland 1987).

Because of their inherent variability, temperate streams are ideal systems for examining the relationship between environmental variation, assemblage structure, and resource use. Precipitation patterns over much of temperate North America are sufficiently variable so that organisms in streams may be subjected to both floods and droughts during their lifetime (Poff and Ward 1989). Thus, the stream biota may frequently be exposed to sources of mortality that are relatively unpredictable (Grossman et al. 1982). A consequence of this phenomenon is that the structure of stream fish assemblages may vary substantially, a result reported by investigators on at least four continents (Mills and Mann 1985, Grossman et al. 1990, Pusey et al. 1993, Hugueny et al. 1995). Such fluctuations suggest that resource limitation may not play as strong a role in the maintenance of assemblage structure or patterns of resource use within stream fish assemblages as it may in more stable systems.

Although environmental variation may have a significant impact on both assemblage structure and resource use within many stream assemblages, its importance as an organizational mechanism is not universal. For example, fishes in some streams exhibit relatively stable abundances (Ross et al. 1985, Matthews et al. 1988, Meffe and Berra 1988). In addition, several investigators suggest that partitioning of limiting spatial resources is an important mechanism for coexistence of stream fishes (Gorman and Karr 1978, Paine et al. 1982, Wynes and Wissing 1982), although,

Baltz and Moyle (1993) have shown that such segregation is not necessarily linked to resource limitation. Nonetheless, Fausch and White (1981), Baltz et al. (1982), Gorman (1988a), and Greenberg (1988) all have documented the presence of competitively induced microhabitat shifts in pairs of coexisting stream fishes. Finally, multiple investigators have shown that predators may strongly affect: (1) assemblage structure (Garman and Nielsen 1982, Lemly 1985, Gilliam et al. 1993), (2) resource use (Power et al. 1985, Fraser et al. 1987, Harvey 1991, Harvey and Stewart 1991), and (3) trophic structure (Power 1992) within lotic habitats. Consequently, at present we are unable to generalize about the mechanisms controlling assemblage structure and resource use within stream fish assemblages.

We assessed the relative effects of environmental variation, habitat limitation, and predator abundance on assemblage structure, microhabitat use, and microhabitat overlap in an assemblage of stream fishes in Coweeta Creek, North Carolina, USA. We did not quantify the effects of food limitation, because Stouder (1990) examined this phenomenon in both drought and non-drought seasons and concluded that neither food limitation nor interspecific interactions played a significant role in the use of trophic resources within this assemblage. Our investigation encompassed a 10-yr time span (1983–1992) and included years with some of the highest and lowest annualized mean daily flows in the last 58 years (e.g., the high water years of 1989, 1992, and 1990 ranked 4th (0.378 m³/s), 5th (0.375 m³/s), and 6th (0.364 m³/s) in flow, whereas the drought years of 1986 and 1988 ranked 58th (0.152 m³/s) and 57th (0.155 m³/s) respectively, Grossman et al. 1995a).

Our analyses has two main parts. The first is a descriptive section which summarizes long-term patterns of: (1) environmental variation, (2) assemblage structure, (3) intraspecific numerical abundance, and (4) spatial resource use by assemblage members. The second is a synthetic portion in which we use these results to test nine hypotheses regarding the relative importance of resource limitation (i.e., total habitat or microhabitat), environmental variation, and predation as mechanisms determining assemblage structure and patterns of resource use within this assemblage. Specifically, if total habitat or microhabitat availability or microhabitat diversity are the primary factors limiting the species in this assemblage, the following hypotheses should be confirmed: (1) aside from seasonal cycles in reproduction and recruitment, assemblage structure and intraspecific numerical abundances of species should not be strongly affected by environmental variation, (2) there should be a positive relationship between the number of species present and total habitat or microhabitat availability or microhabitat diversity, (3) microhabitat overlap among species should be low, (4) microhabitat overlap should be inversely correlated with the number of species present and positively correlated with both total habitat and microhabitat avail-

ability, and (5) changes in the abundance of potential competitors should induce shifts in microhabitat use in the remaining species. Conversely, if environmental variability restricts populations to levels below which habitat limitation (i.e., total habitat or microhabitat) occurs, then Hypotheses 1–4 should be falsified and the following hypotheses should be confirmed: (6) there should be a strong correlation between changes in assemblage structure (and intraspecific numerical abundances) and environmental variation (this prediction is basically the converse of Hypothesis 1), (7) the number of species present should not necessarily be correlated with changes in either total habitat or microhabitat availability (this prediction is the null hypothesis of Hypothesis 2), and (8) microhabitat use and overlap should not be strongly affected by changes in the number of species present, either total habitat or microhabitat availability, or microhabitat diversity. Finally, if predation in a significant organizational mechanism for this assemblage, then assemblage structure, microhabitat use, and microhabitat overlap should be strongly correlated with predator abundances (Hypothesis 9).

METHODS

This analysis extends a previous study by Grossman and Freeman (1987), conducted during the years of 1983–1984. Because these data have been presented previously, we have included them only when necessary.

The study site

Our study area was a 37-m section of Coweeta Creek, a fifth-order stream located in western North Carolina. Based on previous studies, the length of this site should have been sufficient to include the home ranges of the most abundant species (Whitworth and Strange 1983, Hill and Grossman 1987, Petty and Grossman 1996), a prerequisite for studies of assemblage organization (Grossman et al. 1982). The site contains a series of riffle-run-pool habitats, and is visually similar to many other streams in the southern Appalachian region. Riparian vegetation is dominated by rosebay rhododendron (*Rhododendron maximum*), dogwood (*Cornus florida*), mountain laurel (*Kalmia latifolia*) and witch-hazel (*Hammamelis virginiana*).

Environmental variation

To assess the level of environmental variation present in the study site we quantified microhabitat availability (sensu Grossman and Freeman 1987) on a seasonal basis. This information was required for both descriptive and synthetic (i.e., Hypotheses 1–9) aspects of our study. To quantify microhabitat availability, we measured the following variables: average velocity, depth, and the percentage composition of seven substratum categories (bedrock, boulder, cobble, gravel, sand, silt, and debris) in randomly selected 400-cm²

quadrats (Grossman and Freeman 1987). In the first sample, we measured 427 quadrats in the site, (see Grossman and Freeman 1987), however, in subsequent samples the number of quadrats examined ranged from 30 to 50. We were able to reduce the number of quadrats examined per sample based on Grossman and Freeman's (1987) findings regarding sample adequacy, combined with a subjective evaluation of microhabitat diversity in the site. During the course of the study we collected availability data on a single day, either during a two- to four-week period over which we made fish microhabitat measurements (Summer 1983–Autumn 1984), or at the end of shorter (i.e., approximately one to two week) fish measurement periods (Summer 1986–Autumn 1992). Dates of data collection for both fish microhabitat use and microhabitat availability measurements and their assignment to sample follow: Summer 1983, 11 July to 10 August; Autumn 1983, 26 October to 9 November; Spring 1984, 22 March to 24 April; Summer 1984, 5 July to 18 August; Autumn 1984, 26 September to 1 November; Summer 1986, 20 August to 15 September; Autumn 1986, 9 November to 18 November; Spring 1988, 28 April to 27 May; Summer 1988, 5 August to 18 August; Summer 1989, 8 August to 10 August; Autumn 1989, 13 October to 19 October; Spring 1990, 26 April to 11 May; Summer 1990, 4 August to 19 August; and Autumn 1990, 16 October to 1 November; Summer 1992, 26 August to 1 September; and Autumn 1992, 27 October. To further elucidate the role of environmental variation we also classified samples in relation to the drought of 1985–1988: (1) pre-drought (PR) (Spring 1984, Summer 1983, 1984, and Autumn 1983, 1984), (2) drought (D) (Spring 1988, Summer 1986, 1988, Autumn 1986), and (3) post-drought (PO) (Spring 1990, Summer 1989, 1990, 1992, Autumn 1989, 1990, 1992). References to hydrologic periods refer to these classifications. A severe storm occurred prior to the collection of microhabitat availability data for the Autumn 1986 sample; hence, we did not include data from this sample data in analyses requiring microhabitat availability data. We also did not conduct sampling in 1985, 1987, or 1991.

Current velocity and substratum composition were measured in each quadrat using the techniques described in Grossman and Freeman (1987). We measured velocities to the nearest centimeter per second using a Marsh-McBirney electronic current meter. Average velocity was obtained at $0.6 \times$ water-column depth for depths <75 cm (Bovee and Milhous 1978). For deeper quadrats, we calculated average velocity as the mean of measurements made at 0.2 and $0.8 \times$ water-column depth (Bovee and Milhous 1978). Depth was measured to the nearest centimeter and a visual estimate made of the percentage contribution of each substratum category to the total composition of the substratum. We based substratum categories on maximum particle dimensions: bedrock, >30 cm without exposed edges or undersurfaces; boulder, >30 cm with exposed edges

and undersurfaces; cobble, ≤ 30 cm and ≥ 2.5 cm; gravel, ≤ 2.5 cm and ≥ 0.2 cm; sand, < 0.2 cm; and silt, material that was readily suspendable in the water column.

Macroscopic organic material was classified as debris, regardless of size. We also made a single water temperature measurement in the study site during each sample using a mercury thermometer. Additional temperature measurements ($\pm 0.5^\circ\text{C}$) were made in a location slightly upstream from the site using a continuously recording submersible thermograph.

Because the primary manifestation of environmental variation in streams involves changes in streamflow (i.e., floods and droughts), we obtained stream discharge data from the U.S.D.A Forest Service Coweeta Hydrologic Laboratory, Macon County, North Carolina. We used data from Weir 8, which drains Shope Fork, one of two fourth-order tributaries (the other is Ball Creek) of similar size that unite to form Coweeta Creek. During our study the correlation (r) between monthly estimates of mean daily flows for Shope Fork and Ball Creek was 0.99. Our study site was located downstream of the confluence of Shope Fork and Ball Creek, and there were no intervening tributaries. We used gaging data from Weir 8 to determine the frequency of high water events in Coweeta Creek. Between 1982 and 1992, annualized mean daily flows at Weir 8 averaged $0.28 \text{ m}^3/\text{s}$ (range: $0.152\text{--}0.378 \text{ m}^3/\text{s}$, Grossman et al. 1995a). After examining flow recurrence interval data, we arbitrarily classified all flows $\geq 2.1 \text{ m}^3/\text{s}$ as high-flow events. An event of this magnitude represents slightly greater than bank-full discharge, and using the annual maximum series, had a recurrence interval of ~ 1 yr (L. Swift, Coweeta Hydrologic Laboratory, *personal communication*). We examined differences in the frequencies of high-flow events on the basis of both season and hydrologic period using Kruskal-Wallis tests coupled with Tukey-Kramer a posteriori tests ($P = 0.10$). These data consisted of the number of high-flow events during each season across years, and the number of high-flow events during a given year within a hydrologic period. Seasonal flow data were collected as part of a concurrent population dynamics study whose sampling regime necessitated use of the following seasonal classifications: (1) Winter, 3 December to 4 March; (2) Spring, 5 March to 3 June; (3) Summer, 4 June to 2 September, and (4) Autumn, 3 September to 2 December. We used environmental data to test aspects of Hypotheses 1, 2, 4, and 6–8.

We tested for seasonal changes in microhabitat availability by conducting a principal component analysis (PCA) on pooled seasonal availability data using the methods of Grossman and Freeman (1987). Components that had eigenvalues ≥ 1.0 and were ecologically interpretable were retained for further analyses. Hence, our use of the term microhabitat availability represents a multivariate characterization of the physical habitat

of the site in a given sample. We then tested for significant differences in mean seasonal PCA scores (i.e., Spring vs. Summer vs. Autumn) on each component using Kruskal-Wallis tests and Tukey-Kramer a posteriori tests. An identical procedure was used to examine differences based on hydrologic period. Our ability to estimate substratum composition was judged to be $\pm 2\%$ of the actual total. Consequently, we did not consider differences in substratum composition to be significant unless they differed by at least this value.

Effects of environmental variation, habitat limitation, and predation on assemblage structure

To quantify the effects of season, year, and hydrologic period on assemblage structure, we estimated the numerical abundances of fishes visually while making fish microhabitat use measurements. We used an ordinal scale where 0 = 0 specimens observed, 1 = 1–5 specimens observed, 2 = 6–10 specimens observed, 3 = 11–20 specimens observed, and 4 = ≥ 20 specimens observed.

We tested hypotheses involving the effects of both environmental variation and habitat limitation on assemblage structure (Hypotheses 1, 2, 6, 7) by first testing for significant differences in the total number of species per microhabitat sample and the number of abundant species (i.e., only those with abundances ≥ 5 per seasonal microhabitat sample) per sample among both seasons and hydrologic periods. Kruskal-Wallis and Tukey-Kramer tests were used for hypothesis testing ($P = 0.05$). We then conducted correlation analyses (using Spearman's r) on sample means of: (1) water temperature, (2) total habitat and microhabitat availability, (3) microhabitat diversity, (4) total number of species, and (5) the number of abundant species in a sample. Mean water-column depths from microhabitat availability samples were used as an index of total habitat availability (Hypotheses 2 and 7). Mean water-column depth probably is a good index of the total amount of habitat available to fishes, because the site does not contain extensive shallows. (If extensive shallows were present, total habitat availability could be inversely correlated with mean depth if a random sampling regime was used.) We tested the species richness–microhabitat availability hypothesis (Hypothesis 2 and 7), by comparing the total number of species and the number of abundant species to mean sample scores on individual components (i.e., PC1, PC2, or PC4) from the PCA of seasonal microhabitat availability data. To quantify microhabitat diversity, we first calculated the standard deviation of each seasonal microhabitat availability sample on each significant principal component, and then summed these values to produce a single number. We also performed this analysis with two alternative measures of habitat diversity: (1) one that also included a correction factor that incorporated the variance in microhabitat availability data explained by each component, and (2) one based on the unsummed stan-

dard deviations for each significant component (i.e., a separate analysis for each component). These analyses yielded results that either were nonsignificant (individual SDs) or were virtually identical to those of the original analysis; hence, for simplicity we present results only for the original analysis. Spearman's r (r_s) was used for all correlation analyses with $P = 0.10$. We chose a higher value of significance for correlation analyses due to the inherently greater variability of the environmental data being compared (Zar 1974, Grossman 1982). The same criterion was used when we tested for significant differences in: (1) the total number of species and number of abundant species, (2) total habitat availability, or (3) microhabitat diversity across seasons or hydrologic periods (Hypotheses 1, 2, 7).

To quantify long-term patterns of assemblage structure, and compare these results to seasonal and hydrologic variations in total habitat availability (i.e., Hypotheses 1 and 6), we subjected numerical abundance estimates from samples to a cluster analysis using the Unweighted Pair-Group Means algorithm (UPGM) of SAS (1982). We quantified assemblage similarity among seasonal samples using the correlation coefficient option of UPGM (Romesburg 1984). To test for potential predator effects on assemblage structure, we also compared the results of the cluster analysis to the seasonal distribution of potential predators in the site (i.e., *Oncorhynchus mykiss* ≥ 20 cm standard length [SL], and *Ambloplites rupestris* and *Semotilus atromaculatus* ≥ 15 cm SL).

Effects of environmental variation, habitat limitation, and predation on microhabitat use and overlap

To test the predictions of the various organizational mechanisms with respect to microhabitat use and overlap, we quantified microhabitat use by assemblage members using the methods of Grossman and Freeman (1987) (see above for sampling dates). We began by entering the site from a position below its downstream border, snorkeling slowly upstream, and then recording the positions of undisturbed specimens. Microhabitat use measurements were obtained only during daylight hours, because these species appear to be either relatively inactive at night, or occupy similar microhabitats (J. Hill, J. Barrett, A. Thompson, and G. Grossman, *personal observation*). Disturbed fishes exhibited agitated behavior or escape responses, which made them readily recognizable. Our presence did not appear to strongly affect fish behavior, and specimens fed, held position, and occasionally displayed courtship behavior, within 25 cm of the diver. This was true for even the wariest species (i.e., *O. mykiss*). Consequently, we do not believe that our measurement techniques significantly influenced microhabitat use of the fishes observed. Underwater observational techniques have been used for comparable purposes in a variety of lotic systems (e.g., Moyle and Senanayake 1984, Gorman 1988a, Greenberg 1991).

Once we located an undisturbed fish, its position was recorded and the following measurements taken: average velocity, focal point velocity (i.e., at the fishes' position), distance from substratum, distance from shelter (Grossman and Freeman 1987), and depth. We visually estimated the percentage composition of seven substratum categories (bedrock, boulder, cobble, gravel, sand, silt, and debris) in a 400-cm² area, directly under the specimen. The methods used for substratum and average velocity measurements were identical to those used for microhabitat availability measurements.

We evaluated the relative importance of habitat limitation and environmental variation to microhabitat use and overlap (i.e., Hypotheses 3, 4, 7, 8) by first subjecting data from fish microhabitat use samples to a canonical analysis of discriminants (CAD) (see Grossman and Freeman 1987, Grossman and de Sostoa 1994a, b). This technique produced multivariate axes which maximized the among-group (i.e., interspecific) separation of species in microhabitat space. All axes with variance ratios ≥ 1.0 were retained. We then used Kruskal-Wallis and Tukey-Kramer a posteriori tests to detect significant interspecific differences in microhabitat use (i.e., mean score on each canonical axis) within each data set. We considered microhabitat overlap to be high if there were few significant interspecific differences in microhabitat use on the CAD axes. Conversely, we classified microhabitat overlap as low when most species differed significantly in their mean CAD scores. These results were then used to test Hypothesis 3 (i.e., do species generally exhibit low levels of microhabitat overlap?). Because prior research indicated that these species belonged to microhabitat guilds determined by their respective evolutionary histories (Grossman and Freeman 1987), we quantified changes in microhabitat overlap by calculating the mean percentage of significant intra-guild differences in each seasonal sample. This index was derived by dividing the number of significant differences within a guild in seasonal CAD's by the total number of possible differences. These values were summed and then divided by the number of guilds present in a seasonal sample. If microhabitat overlap was high, then the index produced low values (e.g., $<40\%$, range: 0–100%). Conversely, if most species segregated on the basis of microhabitat use (i.e., were habitat limited), then the index yielded high values (e.g., $>70\%$). We employed these data to test Hypotheses 3, 4, and 8, which predict relationships between microhabitat overlap and (1) species richness, (2) microhabitat availability, and (3) microhabitat diversity. Spearman's r ($P = 0.10$) was used for hypothesis testing.

Effects of potential competitors on microhabitat use

To ascertain whether the presence of potential competitors affected either microhabitat use or overlap (Hypothesis 5), we initially compared mean CAD scores of microhabitat use data for a given species across sea-

sons when a potential competitor varied in abundance. Unfortunately, the CAD did not extract any significant components (all variance ratios <1.0) despite many significant differences in univariate data. Rather than reanalyze these intercorrelated data variable by variable, we chose to perform a PCA which did yield interpretable results. We assigned seasons to one of three competitor abundance classes: (1) seasons in which the abundance of a potential competitor was rare (R) in comparison to the species being examined (i.e., from 0–24%), (2) seasons in which the potential competitor was present at intermediate (I) abundance (i.e., 25–49% of the species being examined), and (3) seasons in which the potential competitor was common (C) (i.e., $\geq 50\%$ of the species being examined). The assignment of seasons into one of three competitor abundance classes meant that seven significant statistical outcomes were possible: (1) rare differed significantly from intermediate (i.e., rare \neq intermediate), (2) rare \neq common, (3) intermediate \neq common, (4) rare and intermediate \neq common, (5) rare and common \neq intermediate, (6) rare \neq intermediate and common, and (7) rare \neq intermediate \neq common. However, only four of these results (2, 4, 6, and 7) were consistent with the potential effects of interspecific competition. Consequently, these are the only outcomes presented in the results. We used Kruskal-Wallis tests combined with Tukey-Kramer a posteriori tests to identify significant differences in a species mean PCA score among samples when a potential competitor varied in abundance (i.e., R vs. I vs. C). If a significant difference was observed, we then compared this result to: (1) microhabitat availability data for seasons that differed in competitor abundance and (2) length-related microhabitat use data (Grossman and Freeman 1987, Grossman and Ratajczak 1998) to determine whether the observed shift could be unambiguously attributed to the presence of the competitor. A graphical example of these comparisons is presented in Fig. 1. When significant length-related effects are reported in our results, it should be understood that these findings are contained in a companion paper (Grossman and Ratajczak 1998) that focuses on the descriptive aspects of microhabitat use by assemblage members (i.e., non-random microhabitat use, and seasonal, hydrologic, and length-related variations in microhabitat use). Finally, we compared the raw data among seasons with different competitor abundances to ensure that these differences were both ecologically interpretable and within our estimated detection range (substratum differences $>2\%$). When a difference in a substratum measurement was not $>2\%$, we retained the variable in our tabular presentation of PCA data (Appendix A, Table 4), but did not describe it in the text.

Effects of potential predators on microhabitat use

To assess the relationship between predation and microhabitat use (Hypothesis 9), we compared microhab-

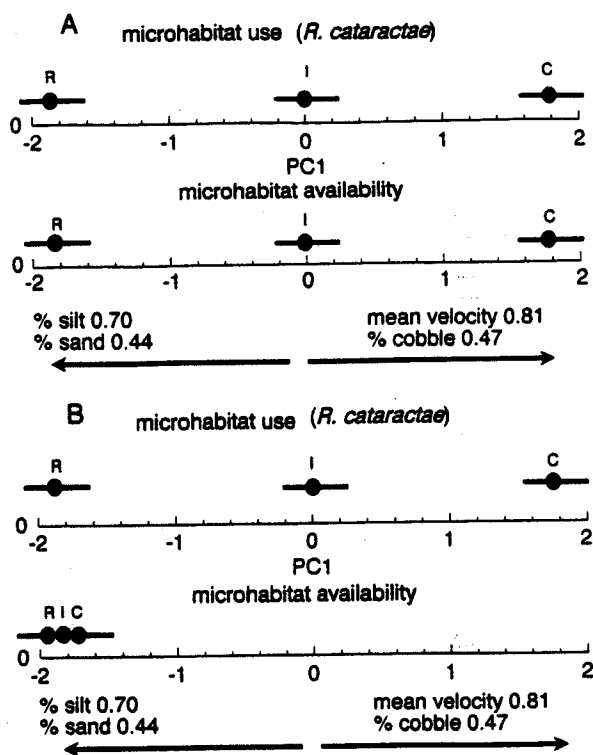


FIG. 1. A graphical representation of hypothetical examples of microhabitat shifts by a species. The axes depict principal components that represent either microhabitat use by a fish species (microhabitat use data) or microhabitat availability data (from random quadrats), from samples that differed in competitor abundance: (R = competitor rare (i.e., competitor abundance = 0–24% of the species being examined), I = competitor intermediate (i.e., competitor abundance = 25–49% of species being examined), C = competitor common (i.e., competitor abundance $\geq 50\%$ of species being examined)). Panel A depicts shifts that were produced by changes in microhabitat availability (i.e., competitor shifts concordant with microhabitat availability shifts). Panel B shows true competitor-linked shifts (i.e., competitor shifts not concordant with microhabitat availability shifts). A similar approach was used to detect shifts that were attributable to changes in the mean length of fishes, and predator effects.

itat use of fishes in samples when potential predators were both present and absent using CAD. Because the daily abundance of predators in the site only ranged from zero to two, we classified samples on the basis of predator presence/absence rather than by numerical abundance. The CAD also failed to extract significant axes from this data set, so we again employed PCA to examine our results. We compared mean PCA scores for seasons when predators were both present and absent using Mann-Whitney tests followed by Tukey-Kramer a posteriori tests. If significant differences were observed, we then compared these results to: (1) microhabitat availability data for seasons when predators were both present and absent and (2) length-related microhabitat use data (Grossman and Freeman 1987, Grossman and Ratajczak 1998) to ensure that the observed shifts were related to the presence of predators.

As with assemblage structure analyses, we considered the following species to be potential predators: *O. mykiss* ≥ 20 cm standard length (SL), and *A. rupestris* and *S. atromaculatus* ≥ 15 cm SL. We did not include terrestrial or avian predators in analyses, because they were rare (see Grossman and Freeman 1987).

RESULTS

Environmental variation

Water temperatures differed among years within a season (Table 1). Temperatures during Spring 1988 and 1990 were significantly warmer than those of Spring 1984. Summer 1988 and 1990 temperatures were significantly warmer than those of Summer 1989 and 1992, whereas water temperatures in Autumn 1984 were warmer than those of Autumn 1983 and 1990. In general, the drought only produced moderate increases in water temperature. It is also likely that some of the observed differences observed were due to disparities in sampling dates (i.e., Spring and Autumn data, Table 1).

Microhabitat availability data demonstrated that the site displayed significant amounts of environmental variation during our study. The PCA extracted four significant components that explained 68% of the variance in the microhabitat availability data set. Only components one and four, however, produced ecologically interpretable information for seasonal microhabitat data (Table 2). Component one showed that Spring samples possessed the highest velocities, greatest amounts of cobble and gravel, and lowest quantities of depositional substrata, whereas Summer samples exhibited the lowest velocities, lowest quantities of gravel and cobble, and highest amounts of depositional substrata (Table 2). Autumn samples displayed intermediate values for these parameters, and did not differ significantly from either Spring or Summer samples. Component four indicated that Summer samples possessed shallower depths with higher amounts of boulders than Autumn samples. Seasonal habitat availability analyses probably were affected by unequal sampling effort (e.g., Autumn data did not include any D samples).

Our analyses of hydrologic period data indicated that PO samples had the highest velocities, greatest amounts of large erosional substrata, and lowest quantities of depositional substrata (Table 2). Conversely, D samples had the lowest velocities, lowest quantities of erosional substrata, and the greatest amounts of depositional substrata. Pre-drought samples were intermediate between D and PO samples, although they did not differ significantly from D on component 1 (Table 2). Hydrologic analyses produced a greater number of significant differences among samples (i.e., 5 of 6) than seasonal analyses (2 of 6, Table 2). This suggests that hydrologically linked environmental variation had a greater

impact on microhabitat availability than did seasonal patterns of variation.

Despite the substantial level of environmental variability observed within the site, there were few apparent temporal trends in total habitat availability or microhabitat diversity (Fig. 2). Neither of these parameters varied significantly on a seasonal basis. Total habitat availability was significantly greater during PO than in either PR or D samples ($P = 0.07$). There were no significant differences in microhabitat diversity during the three hydrologic periods. Water temperature was negatively correlated with depth ($r_s = -0.46$, $P < 0.09$), and positively correlated with microhabitat diversity ($r_s = 0.47$, $P < 0.08$).

Our analysis of environmental variation within the site also showed that high-flow events ($N = 34$) were not evenly distributed over the years of the study period (Fig. 3). Although the mean number of high-flow events did not differ significantly among seasons, there were significantly fewer high-flow events per year during D ($\bar{X} = 0.7 \pm 1$ SD) than in either PR ($\bar{X} = 4.3 \pm 2.1$ SD) or PO ($\bar{X} = 4.5 \pm 3.1$ SD) periods.

Effects of environmental variation, habitat limitation, and predation on assemblage structure

We observed a total of 16 species in the study site (Table 3). The total number of species per sample ranged from a high of 13 species in Autumn 1986 to a low of 7 species in Summer 1983, 1990, and Spring 1984 (Fig. 2). There were no significant differences in the mean total number of species among seasonal samples, which ranged from 10.0 in Autumn to 8.7 in Spring (Fig. 2). We obtained a similar result for the mean number of abundant species per seasonal sample (range 6.6–7.0 species). In hydrologic analyses, the total number of species was significantly higher during D ($\bar{X} = 11.3$, $p < 0.10$) than in PR collections ($\bar{X} = 8.0$). Samples from PO were intermediate ($\bar{X} = 9.3$), and did not differ significantly from either PR or D samples. There were no significant differences in the number of abundant species during the three hydrologic periods. These results indicate that environmental variation in the form of the drought had a substantial effect on the total number of species present in the site, and hence, the results contradict the prediction of Hypothesis 1 and support Hypothesis 6.

The correlation analysis between environmental variables and the number of species in the site yielded limited results. There were no significant correlations between either the total number of species or the number of abundant species, and (1) water temperature, (2) microhabitat availability (i.e., score of a seasonal sample on PC1, PC2, or PC4), or (3) microhabitat diversity. In addition, the number of abundant species was not significantly correlated with total habitat availability. However, the total number of species was inversely correlated with total habitat availability (i.e., depth, $r_s = -0.48$, $P < 0.07$), and not surprisingly, positively

TABLE 1. Seasonal water temperature measurements made during fish microhabitat

Spring			Summer	
Year	Dates	Temperature ($\bar{X} \pm SD$)	Year	
1984	22 Mar to 24 Apr	8.7 \pm 0.9 ^b	1983	11 Jul
1988	28 Apr to 27 May	11.6 \pm 0.8 ^a	1984	5 Jul
1990	26 Apr to 11 May	12.5 \pm 2.1 ^a	1986	20 Au
			1988	5 Au
			1989	8 Au
			1990	4 Au
			1992	26 Au

Notes: We compared seasonal means using Kruskal-Wallis and Tukey-Kramer a with the same superscript are not significantly different. Samples were not collected for further details.

correlated with the number of abundant species ($r_s = 0.50$, $P < 0.06$). The lack of a positive correlation between the total number of species or number of abundant species and total habitat or microhabitat availability or microhabitat diversity indicates that Hypothesis 2 can be rejected. In fact, the inverse correlation between the total number of species and total habitat availability runs counter to the prediction of the habitat limitation hypothesis, and consequently, lends support to the environmental variation hypothesis (i.e., Hypothesis 7).

The cluster analysis grouped numerical abundance data on the basis of hydrologic period rather than season or year (Fig. 4). Hence, hydrologic variation in the site had a stronger impact on this assemblage than seasonal or annual cycles of habitat availability. With the exception of Autumn 1984, and Summer 1989 and 1990 data, samples from each hydrologic period were located in separate terminal clusters, although in the case of both D and PO data, more than one cluster was produced for each period. Autumn 1984 (PR) grouped with PO samples, whereas Summer 1989 (PO) and 1990 (PO) clustered with PR samples. Drought samples possessed the most distinct assemblage structure, whereas PR and PO periods were more similar (Fig. 4). Intraspecific numerical abundance data suggested that these relationships were produced by changes in the abundance of several species (e.g., *N. micropogon*, *E. blennioides*, *N. leuciodus*) that either first appeared (*N. micropogon*, *N. leuciodus*, *P. evades* and *Lepomis* sp.) or emigrated (*E. blennioides*) during the drought (Table 3). Patterns within a hydrologic period were similar to those among periods. Seasonal assemblage structure patterns during the PR and PO period were the most similar, whereas D samples were the least similar (Fig. 4). Summer samples for both D and PO periods clustered separately from other seasons in these periods. These differences probably were caused by the annual emigration of *C. anomalum* and *A. rupestris* from the site during summer (Table 3). In conclusion, results from both cluster and correlation analyses suggest that Hypotheses 1 and 2 (i.e., environmental variation has little effect on assemblage structure, or intraspecific

variation in abundance findings support environmental variation hypothesis).

Predators (i.e., ≥ 15 cm SL and C in 9 of a total of 16 were present in months as, they were not (two of six) or D present, predators the maximum number of predators per sampling was two. No specific numerical abundance was positively or negatively correlated in the site (i.e., $P > 0.05$); Fig. 4, T predation had a significant effect on assemblage.

Intraspecific variation

As expected, given the structure, most of the differences could be attributed to the drought (Table 3). In contrast to the habitat limitation hypothesis, however, the drought appeared to affect abundance on many species. For example, *C. fundulus*, *O. mykiss*, *A. rupestris*, *N. leuciodus*, *P. evades*, *Lepomis* sp., *E. blennioides*, *N. micropogon*, *N. leuciodus*, *P. evades* and *Lepomis* sp. abundance during drought also had significant differences. *N. leuciodus*, neither present prior to the increase in abundance of the PO samples (Table 3) first recorded during drought was found during drought. Several rare species (*L. cinctus*, *A. rupestris*, *C. anomalum*, *P. evades*) [Summer samples] were found during D. All species served during the

Autumn		Temperature ($\bar{X} \pm \text{SD}$)
Year	Dates	
1983	26 Oct to 9 Nov	10.6 ± 0.7^b
1984	26 Sep to 1 Nov	14.0 ± 1.8^a
1986	9 Nov to 19 Nov	11.7 ± 2.1^{ab}
1989	13 Oct to 19 Oct	13.3 ± 1.3^{ab}
1990	16 Oct to 1 Nov	10.4 ± 1.9^b
1992	27 Oct	9.5^{ab}

Despite the increases in abundance displayed by many species during and after the drought, the remaining species did not respond in a similar manner. In fact, a majority of resident benthic species either did not increase in abundance (e.g., *C. bairdi*, *R. catartatae*, and *C. anomalum*) or appeared to emigrate from the study site (i.e., *E. blennioides*) during the drought (Table 3). *Etheostoma blennioides* returned to the study site during PO although its abundance was lower than in PR. We only observed *A. rupestris* and *Cyprinella galactura* ($N = 1$) during the PO period (Table 3).

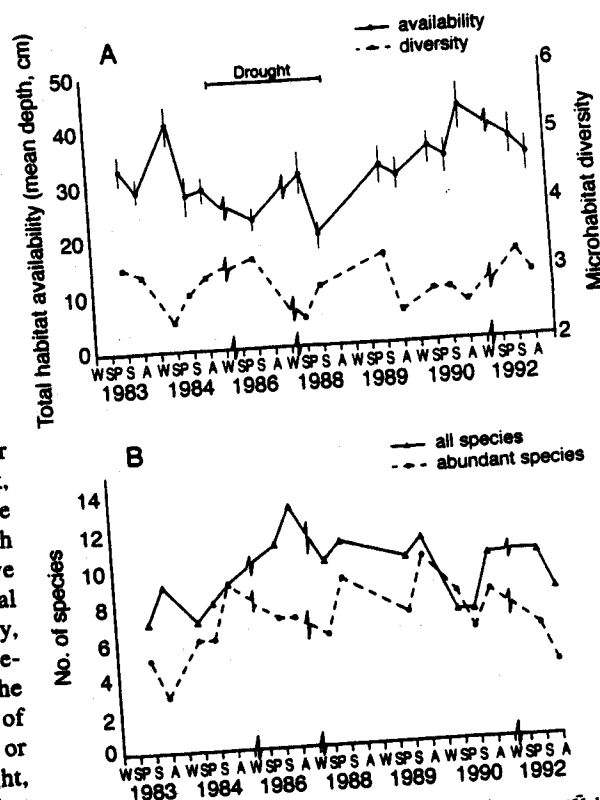


FIG. 2. (A) Variations in total habitat availability (\bar{X} depth ± 1 SD) and microhabitat diversity (pooled standard deviations of PCs 1, 2, and 4), and (B) variations in total number of species present, and the number of abundant species (abundance ≥ 5) in the study site during the course of our study. Samples were not collected in 1985, 1987, and 1991.

Effects of environmental variation, habitat limitation, and predation on microhabitat use and overlap

Canonical analysis of discriminants (CAD) produced significant axes from all fish microhabitat use samples. In nine of eleven samples (PR samples were presented in Grossman and Freeman 1987) a single axis was extracted, whereas two axes were derived from the remaining two samples. Although some species did not always fall neatly into a group along the CAD axes,

TABLE 2. PCA test for significant differences in microhabitat availability among both seasons and hydrologic periods.

Significant component	Variance explained (%)	Variables (loadings in parentheses) for significant components	Significant differences	
			Season	Hydrologic period
1	25	% silt (-0.71), % debris (-0.53), % sand (-0.44), mean velocity (0.85), % cobble (0.51), % gravel (0.41)	Sp > S	PO > PR, D
2	18	% cobble (-0.63), % gravel (-0.56), % bedrock (0.60), % boulder (0.58)	NS	PO > PR > D
4	12	% boulder (-0.51), depth (0.44)	A > S	NS

Notes: Seasons and hydrologic periods are abbreviated as follows: Sp = Spring, S = Summer, A = Autumn, PR = Pre-drought, D = Drought, PO = Post-drought. We tested for significant differences in mean component scores of seasons or hydrologic periods using Kruskal-Wallis tests followed by Tukey-Kramer a posteriori tests. See *Methods* for further details. We only present data for variables with loadings $\geq |0.40|$ on components.

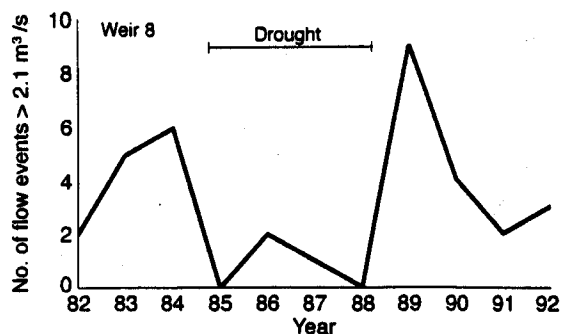


FIG. 3. The number of high-flow events (i.e., ≥ 2.1 m³/s) observed between 1982 and 1992 at Weir 8, Shope Fork. An event of this magnitude has a recurrence interval of one year in Coweeta Creek.

we observed two general patterns of interspecific microhabitat use (Figs. 5 and 6): (1) a two-guild structure including benthic and mid-water-column guilds (S90, S92, A92) that occasionally included a single species occupying the lower water column (S86, S89) and (2) a three-guild structure including, benthic, lower-water-column, and mid-water-column guilds (A86, Sp88, S88, A89, Sp90, A90). Guilds were defined as groups of species that generally did not differ significantly on canonical axes of microhabitat use data, e.g., Fig. 5. Species comprising the benthic guild (*C. bairdi*, *E. blennioides*, *H. nigricans*, and large [i.e., >45 mm] *R. cataractae*) were found: (1) on or close to the substratum and shelter, (2) at lower focal point velocities, and (3) generally in shallower water than members of the water-column guilds. In contrast, members of the mid-water-column guild (*C. funduloides*, *L. coccogenis*, *N.*

leuciodus, *O. mykiss*, and *S. atromaculatus*) characteristically occupied: (1) microhabitats far from the substratum and shelter, (2) higher focal point velocities, and (3) typically greater depths than benthic species. Members of the lower-water-column guild included *A. rupestris*, *C. anomalum*, *N. micropogon*, and small (i.e., <45 mm) *R. cataractae*. These species occupied microhabitats with characteristics intermediate between benthic and mid-water-column guilds. Members of the benthic and mid-water-column guilds generally were statistically distinguishable from each other. In contrast, members of the lower-water-column guild frequently were not separable from one or more members of either the benthic or mid-water-column guilds (Figs. 5 and 6). Given the high level of microhabitat overlap exhibited within this assemblage (Figs. 5 and 6), we can reject Hypothesis 3.

Species generally remained within a single microhabitat guild during the study; however, we also observed exceptions to this pattern (e.g., *H. nigricans* in A89, Sp90 and A90, *C. funduloides* in Sp88 and A89, and *N. micropogon* in S89). Although most members of the same guild did not exhibit significant differences in microhabitat use, several within-guild differences did occur (Figs. 5 and 6). Within the mid-water-column guild, *L. coccogenis* typically occurred farther from both shelter and the substratum, in deeper locations with higher velocities than *C. funduloides*. During Summer 1988, *H. nigricans* (benthic guild) occupied deeper areas with greater quantities of boulders than either *C. bairdi* or *R. cataractae*. We obtained similar results when mid-water-column guild members *L. coccogenis* and *S. atromaculatus* (i.e., deeper with more

TABLE 3. Visual numerical abundance estimates for species in the study site. Abundance categories are as follows: 0, 0 specimens observed; 1, 1–5 specimens observed; 2, 6–10 specimens observed; 3, 11–20 specimens observed; 4,

Species	Residency class	Summer 1983	Autumn 1983	Spring 1984	Summer 1984	Autumn 1984	Summer 1986
<i>Ambloplites rupestris</i>	S	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
<i>Campostoma anomalum</i> †	S	0.0 ± 0.0	0.7 ± 0.5	1.0 ± 0.5	0.0 ± 0.0	2.1 ± 1.3	0.0 ± 0.0
<i>Clinostomus funduloides</i>	R	3.0 ± 1.4	3.1 ± 0.2	3.8 ± 0.3	2.6 ± 1.1	4.0 ± 0.0	4.0 ± 0.0
<i>Cottus bairdi</i>	R	2.1 ± 0.0	2.3 ± 0.8	1.9 ± 0.6	3.0 ± 0.0	3.0 ± 0.6	4.0 ± 0.0
<i>Etheostoma blennioides</i>	R	0.5 ± 0.0	0.3 ± 0.5	0.1 ± 0.3	0.8 ± 0.5	1.0 ± 0.0	0.7 ± 0.5
<i>Hypentelium nigricans</i>	R	0.0 ± 0.0	0.3 ± 0.5	0.0 ± 0.0	0.2 ± 0.5	0.5 ± 0.6	0.7 ± 0.5
<i>Nocomis micropogon</i>	S	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	3.5 ± 0.6
<i>Luxilus coccogenis</i>	R	0.5 ± 0.6	0.6 ± 0.5	0.5 ± 0.5	0.4 ± 0.5	1.6 ± 0.8	0.5 ± 0.6
<i>Notropis leuciodus</i>	S	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.7 ± 1.0
<i>Oncorhynchus mykiss</i>	R	0.5 ± 0.6	0.7 ± 0.5	0.9 ± 0.3	1.0 ± 0.0	1.1 ± 0.4	1.3 ± 0.5
<i>Percina evades</i>	S	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.5 ± 0.6
<i>Rhinichthys cataractae</i>	R	0.5 ± 0.6	0.7 ± 0.5	0.9 ± 0.3	1.0 ± 0.0	1.1 ± 0.4	1.3 ± 0.5
<i>Semotilus atromaculatus</i>	R	1.0 ± 0.0	0.5 ± 0.6	0.0 ± 0.0	0.4 ± 0.5	0.6 ± 0.5	1.7 ± 0.5
Mean abundance (± SD)		0.6 ± 0.9	0.7 ± 0.9	0.7 ± 1.1	0.7 ± 1.0	1.2 ± 1.2	1.5 ± 1.4
Number of days fish abundance estimates were made		4	7	8	5	7	4
Number of days fish microhabitat use measurements were made		5	7	8	7	7	4

† *Lepomis* sp., *Moostoma duquesnei* and *Cyprinella galactura* also were occasionally observed in the study site.

‡ This species was misidentified as *C. oligolepis* in Grossman and Freeman (1987) and Freeman et al. (1988).

boulders) were compared to *O. mykiss* and *C. funduloides* (shallower with fewer boulders). Significant intra-guild differences also were found in Autumn 1989 when: (1) small *R. cataractae* (lower-water-column guild) occupied shallower locations with more silt than *H. nigricans*, *C. anomalum*, *A. rupestris*, and *N. micropogon*, (2) *H. nigricans* occurred in deeper locations with less silt than *C. bairdi*, and (3) *N. micropogon* was found in deeper microhabitats with less silt than *C. funduloides*.

We detected a variety of significant relationships among the number of guilds in a season, total number of species in a sample period, and microhabitat characteristics (i.e., tests of Hypotheses 3, 4, and 8). First, with the exception of Summer 1986, samples with two guilds only occurred in PO samples, 57% of which exhibited this guild structure. Conversely, all D samples possessed three microhabitat guilds, although 43% of PO samples also displayed three guilds. (All PR samples contained two microhabitat guilds, Grossman and Freeman 1987.) Finally, the number of guilds in a sample was associated with the number of abundant species present; samples with two guilds possessed a mean of 5.75 species, whereas, three-guild samples had a mean of 7.8 species.

The level of microhabitat overlap exhibited by assemblage members was high, and the mean percentage of significant intra-guild differences across all samples was only 26% (Fig. 7), a value that did not differ significantly on the basis of either season or hydrologic period. This result confirms our earlier finding that Hypothesis 3 can be rejected. In addition, there were no significant correlations between the mean percentage

of significant intra-guild differences and: (1) water temperature, (2) either total habitat or microhabitat availability, (3) total number species, or (4) number of abundant species. This evidence provides support for Hypothesis 7, and leads us to reject Hypothesis 4. Finally, the mean percentage of significant intra-guild differences was inversely correlated with microhabitat diversity ($r_s = -0.54$, $P < 0.04$), although this relationship was not detected in correlation analyses between the mean percentage of significant intra-guild differences and the standard deviations of seasonal samples on PC1, PC2, or PC4. Nonetheless, the result does lend some support to the general, habitat limitation hypothesis.

Effects of potential competitors on microhabitat use

Sample sizes were adequate to test for competitor-induced shifts in microhabitat use for 15 species pairs. The majority of microhabitat shifts observed (i.e., 9 of 15) were unambiguously attributable to changes in microhabitat availability or length-related shifts in microhabitat use, rather than variations in the abundance of potential competitors (Table 4, Appendix A). None of the remaining six shifts were strong and the amount of variance in microhabitat use explained by these components was low, averaging only 16% (range 10–37%), with only one value >15%. Thus, even when potential competitor effects were detected, they only involved minor axes of microhabitat use (Table 4). Consequently, this lack of competitor-linked shifts for most species indicates that habitat limitation probably was not an important structuring mechanism for this assemblage (i.e., reject Hypothesis 5).

>20 specimens observed.† Species were assigned to a residency class based on the criteria of Freeman et al. (1988); R = resident, S = seasonal.

Autumn 1986	Spring 1988	Summer 1988	Summer 1989	Autumn 1989	Spring 1990	Summer 1990	Autumn 1990	Summer 1992	Autumn 1992
0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.8 ± 0.5	0.0 ± 0.0	0.0 ± 0.0	1.0 ± 0.0	0.0 ± 0.0	1.0
3.3 ± 0.6	4.0 ± 0.0	1.7 ± 0.5	0.3 ± 0.6	3.7 ± 0.5	1.5 ± 1.0	0.0 ± 0.0	1.7 ± 0.6	0.3 ± 0.6	2.0
4.0 ± 0.0	4.0 ± 0.0	4.0 ± 0.0	4.0 ± 0.0	4.0 ± 0.0	4.0 ± 0.0	4.0 ± 0.0	4.0 ± 0.0	4.0 ± 0.0	4.0
3.0 ± 0.0	2.7 ± 0.5	3.0 ± 0.8	2.7 ± 0.6	3.3 ± 0.6	3.0 ± 0.0	2.5 ± 0.7	3.0 ± 0.0	2.0 ± 1.0	2.0
0.7 ± 0.6	0.0 ± 0.0	0.0 ± 0.0	0.3 ± 0.6	0.5 ± 0.6	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0
0.7 ± 0.0	1.0 ± 0.0	1.0 ± 0.0	0.7 ± 0.6	1.0 ± 0.0	0.7 ± 0.5	1.0 ± 0.0	0.7 ± 0.6	0.7 ± 0.6	1.0
3.7 ± 0.6	3.5 ± 0.6	3.0 ± 0.0	1.3 ± 0.6	1.0 ± 0.8	1.3 ± 1.0	0.3 ± 0.6	0.7 ± 0.6	0.7 ± 0.6	0.0
2.0 ± 0.0	3.3 ± 0.5	1.5 ± 0.6	1.0 ± 1.0	3.0 ± 0.0	2.3 ± 0.5	0.0 ± 0.0	2.3 ± 1.7	3.7 ± 0.6	4.0
1.3 ± 0.6	1.0 ± 0.8	0.3 ± 0.5	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.3 ± 0.6	1.0
1.7 ± 0.6	1.7 ± 1.0	1.7 ± 0.5	3.0 ± 0.0	2.7 ± 0.6	1.3 ± 0.5	1.7 ± 0.6	2.0 ± 0.0	3.0 ± 1.0	3.0
0.7 ± 0.6	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0
0.7 ± 0.6	1.0 ± 1.1	2.0 ± 0.8	1.0 ± 0.0	1.5 ± 0.7	0.0 ± 0.0	1.0 ± 0.0	1.3 ± 0.6	2.0 ± 1.0	0.0
0.3 ± 0.6	0.5 ± 0.6	2.0 ± 0.8	0.7 ± 0.6	1.0 ± 0.0	1.3 ± 1.0	1.3 ± 0.6	0.7 ± 0.6	1.3 ± 0.6	0.0
1.7 ± 1.4	1.7 ± 1.6	1.6 ± 1.3	1.2 ± 1.3	1.7 ± 1.4	1.2 ± 1.3	0.9 ± 1.2	1.3 ± 1.2	1.4 ± 1.4	1.4 ± 1.5
3	4	4	3	4	4	3	3	3	1
3	4	4	3	4	4	4	4	3	1

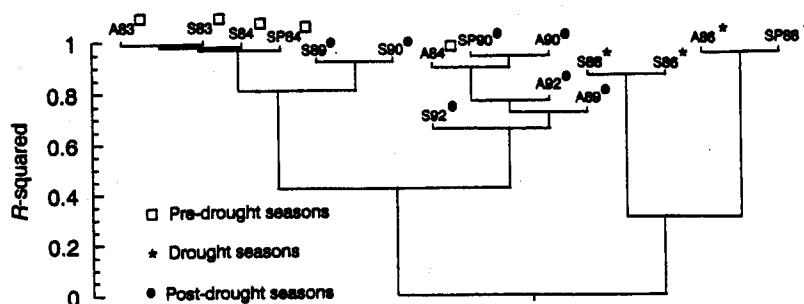


FIG. 4. A dendrogram of seasonal (1983–1992) Coweeta Creek assemblage structure (i.e., numerical abundances of species) samples based on the Unweighted Pair-Group Means algorithm. Sample abbreviations denote seasons and years (Sp = spring, S = summer, and A = autumn). R^2 represents the level of similarity among samples and is interpreted as the square of the correlation coefficient among samples.

Nonetheless, we will discuss the six shifts in microhabitat use associated with changes in the abundance of potential competitors: (1) *C. funduloides* vs. *N. micropogon*, (2) *C. funduloides* vs. *O. mykiss*, (3) *C. funduloides* vs. *S. atromaculatus*, (4) *L. coccogenis* vs. *N. micropogon*, (5) *O. mykiss* vs. *S. atromaculatus*, and (6) *S. atromaculatus* vs. *N. micropogon*. Five of the six shifts involved two species as the potential competitor (*N. micropogon* and *S. atromaculatus*); species whose peak abundances occurred during the drought (Table 3) when microhabitat availability also differed significantly from PR and PO seasons (Table 2). Consequently, even these results were correlated with variations in microhabitat availability (Table 4, Appendix A), and could not be unambiguously linked to abundance variations of potential competitors.

Of the changes related to variations in the abundance of *N. micropogon*, when *N. micropogon* was common or present at intermediate abundance, *L. coccogenis* occurred at higher average and focal point velocities, farther from the substratum over less sand and silt than when *N. micropogon* was rare (Table 4). In addition, this species also occupied shallower microhabitats with more cobble and gravel and less boulder when *N. micropogon* was common than when it was rare or occurred at intermediate abundance. Changes in microhabitat availability and length-related shifts in microhabitat use could have affected these results, because when *N. micropogon* was present at intermediate abundances the habitat possessed higher average velocities with more cobble and less sand and silt than when this species was common (Appendix 1). The mean length of *L. coccogenis* also was significantly larger in seasons when *N. micropogon* was present at intermediate abundances than when it was common or rare (Table 4). Pooled length-related microhabitat use data showed that larger *L. coccogenis* generally occupied deeper locations, over less cobble and boulder than smaller members of this species (Grossman and Ratajczak 1998). During Autumn 1986, larger *L. coccogenis* also were found farther from the substratum, at faster average and focal-point velocities than smaller members of this species, although the opposite result was ob-

served in several PO samples (Grossman and Ratajczak 1998). Consequently, although *L. coccogenis* exhibited some evidence of a microhabitat shift in the absence of *N. micropogon*, it is likely that changes in both microhabitat availability and length-related microhabitat shifts influenced this result.

Similarly, when *N. micropogon* was common, *S. atromaculatus* occurred over more bedrock and less gravel than when *N. micropogon* was rare (Table 4). Once again, these results may have been affected by variations in microhabitat availability, because the habitat had higher average velocities and more cobble and less sand when *N. micropogon* was common than when it was rare (Appendix A). The only shift that was not associated with changes in habitat availability occurred between *C. funduloides* and *N. micropogon*. When *N. micropogon* was common and present at intermediate abundances, *C. funduloides* occurred over less boulder than when *N. micropogon* was rare. The fitness consequences of this shift are uncertain.

Competition-related shifts associated with *S. atromaculatus* were as follows. First, when *S. atromaculatus* was common, *O. mykiss* occurred closer to the substratum over slightly more cobble (intermediate only) and gravel (rare only), and less boulder, than when *S. atromaculatus* was rare or intermediate in abundance. Nonetheless, the habitat was shallower with lower average velocities when *S. atromaculatus* was common than when it was rare or intermediate (Appendix A). Second, when *S. atromaculatus* was common, *C. funduloides* occupied microhabitats with more bedrock and less gravel and boulder than when *S. atromaculatus* was present at intermediate abundances. An identical relationship was observed between seasons when *S. atromaculatus* was present at intermediate abundances (more bedrock and less gravel and boulder) and rare. However, when *S. atromaculatus* was common, the habitat contained more bedrock and boulder and less gravel than when *S. atromaculatus* was rare or present at intermediate abundances (Table 4, Appendix A). In addition, *C. funduloides* was significantly smaller in length when *S. atromaculatus* was common than when this species was rare or present at inter-

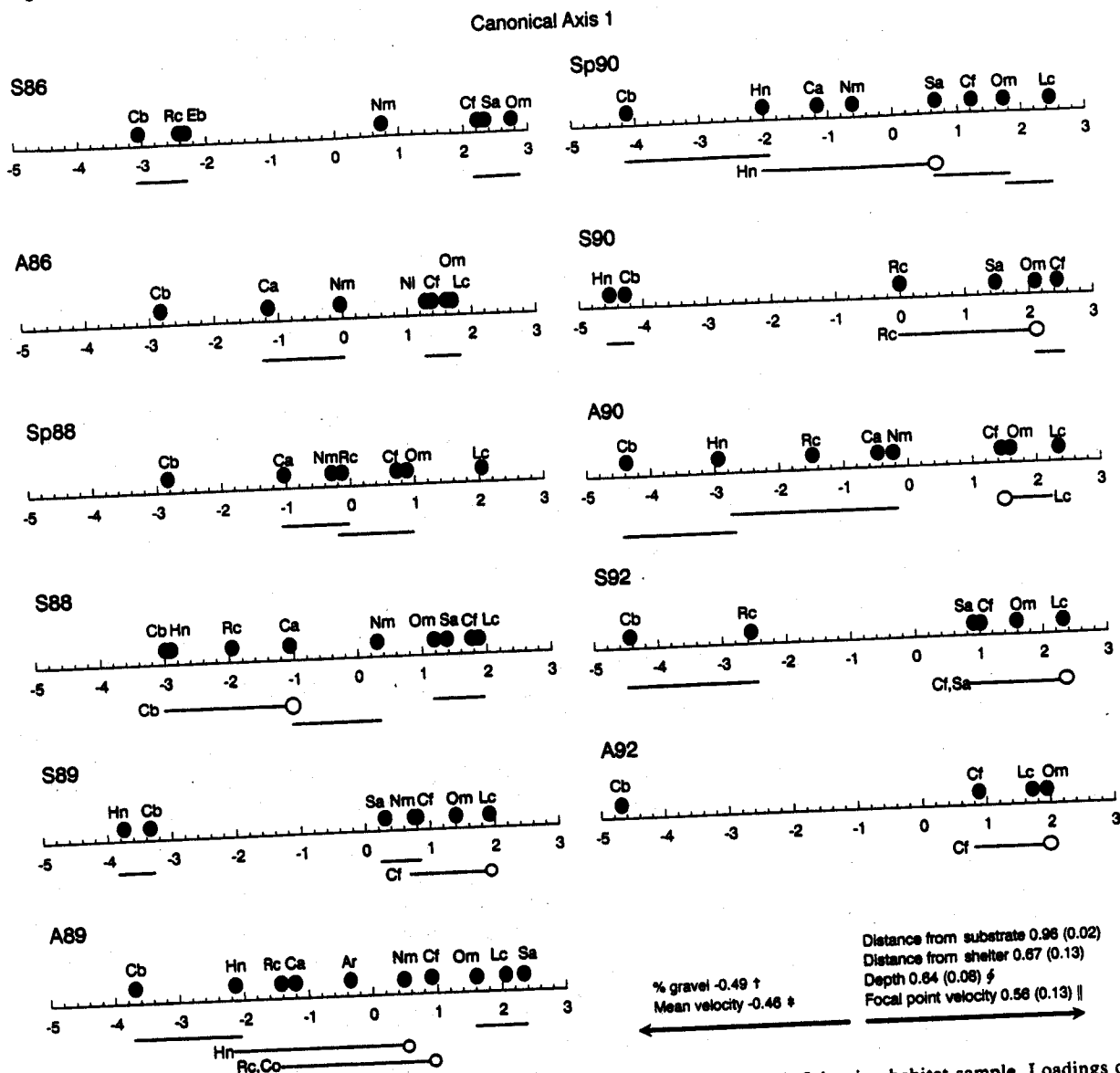


FIG. 5. Significant axes from the CAD of interspecific microhabitat use for each fish microhabitat sample. Loadings of variables for all axes shown are given at the bottom right of the figure. Species abbreviations are as follows: Ar = *A. rupestris*, Ca = *C. anomalum*, Cb = *C. bairdi*, Cf = *C. funduloides*, Eb = *E. blennioides*, Hn = *H. nigricans*, Lc = *L. coccogenis*, Nm = *N. micropogon*, Nl = *N. leuciodus*, Om = *O. mykiss*, Rc = *R. cataractae*, Sa = *S. atromaculatus*. Species connected by a solid line did not differ significantly in microhabitat use using Kruskal-Wallis and Tukey-Kramer a posteriori tests. An open circle on the line indicates that the species above differed significantly from the species whose abbreviation is listed at the end of the line (e.g., see Ca and Cb in S88). Values adjacent to physical variables represent the mean loading of that variable on the component across all seasonal samples (SD in parentheses). Guilds were defined as groups of species whose patterns of microhabitat use did not differ significantly in a seasonal sample. Samples were not collected during 1985, 1987, and 1991.

† Percentage gravel was only significantly correlated with axis 1 during A92.

‡ Mean velocity was only significantly correlated with axis 1 during A86.

§ Depth was not significantly correlated with axis 1 during A86, Sp88, S88, S90, and A92.

|| Focal point velocity was not significantly correlated with axis 1 during Sp88, S92.

mediate abundances. In one season, smaller *C. funduloides* occurred over more bedrock and less gravel than larger members of this species although we also obtained contrasting results (i.e., less bedrock and more boulder, Grossman and Ratajczak 1998).

The last microhabitat shift correlated with variations

in the abundance of a potential competitor occurred between *O. mykiss* and *C. funduloides*. When *O. mykiss* was common, *C. funduloides* occurred in deeper microhabitats farther from shelter and the substratum over less bedrock than when *O. mykiss* was rare or intermediate in abundance. However, when *O. mykiss* was

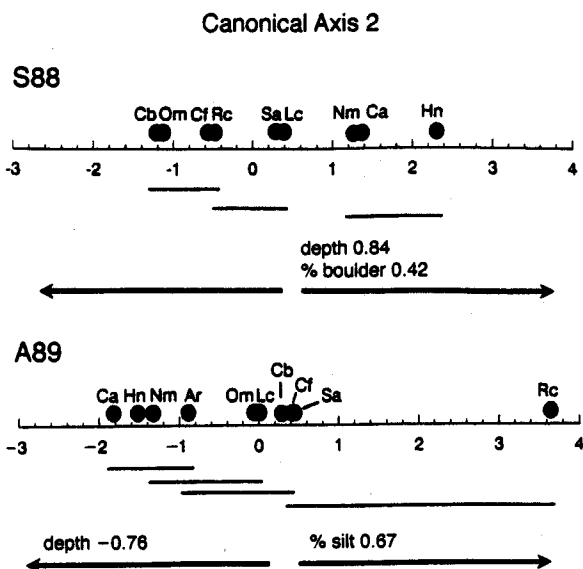


FIG. 6. Seasons for which a second significant canonical axis was extracted from interspecific microhabitat data. See Fig. 5 for further details.

common, the habitat had greater mean depth and higher average velocity than when *O. mykiss* was present at intermediate abundances (Table 4, Appendix A). In addition, *C. funduloides* were significantly smaller when *O. mykiss* was common or present at intermediate abundances than when it was rare (Table 4), and smaller *C. funduloides* occurred farther from shelter than larger specimens (Grossman and Ratajczak 1998).

Our analysis of the effects of interspecific competition on microhabitat use was strongly affected by the fact that both microhabitat availability and mean lengths of the species being examined varied concurrently with competitor abundance. Thus, although six of fifteen interspecific comparisons elucidated shifts that could have been related to interspecific competition, the majority of evidence suggests that other factors (e.g., microhabitat availability and length-related

shifts in microhabitat use) played a stronger role in the production of these differences. Consequently, we do not believe that habitat limitation, in the form of interspecific competition for spatial resources, had a strong effect on microhabitat use by assemblage members.

Effects of predators on microhabitat use

Our analyses of predator-related shifts in microhabitat use (i.e., Hypothesis 9) indicated that most shifts between samples when predators were present (henceforth predator samples) and absent (predator-absent samples) were due to significant differences in either microhabitat availability (predator vs. predator-absent) or standard length of the potential prey species (Table 5, Appendix B). In fact, six of the nine predator samples occurred during the hydrologic period with the most distinct microhabitat availability characteristics (i.e., PO), whereas only one of seven predator-absent samples occurred during PO. Hence, although we have presented all data in Table 5, we only describe results that were at least partially attributable to the presence or absence of predators.

Three of four benthic species exhibited microhabitat shifts in predator analyses. The differences displayed by the three species (i.e., *C. bairdi*, *C. anomalum*, and *R. cataractae*) all were attributable to either length-related shifts in microhabitat use or seasonal (i.e., predator-present vs. predator-absent) changes in microhabitat availability (Table 5, Appendix B). *Etheostoma blennioides* did not exhibit significant differences in microhabitat use between predator-absent and predator seasons.

Predator-related shifts in microhabitat use by water-column species were similar to those observed in benthic fishes. In predator samples, *L. coccogenis* occupied deeper microhabitats with more boulder and less cobble and gravel (Table 5). The difference in depth may have been caused by length-related microhabitat shifts (Table 5), because larger *L. coccogenis* tended to be more

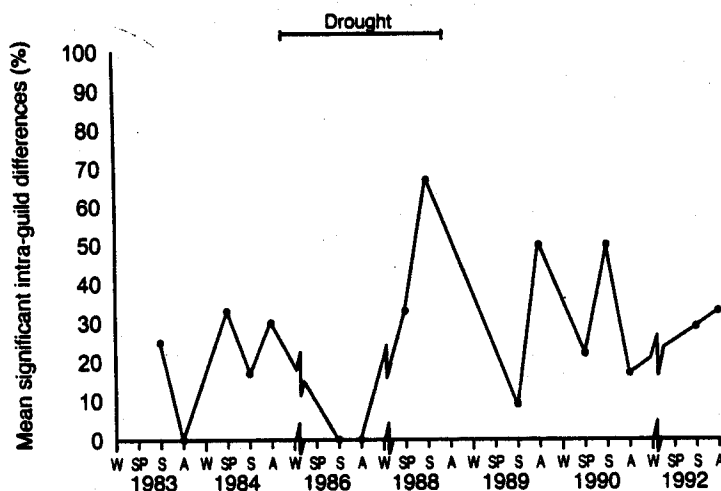


FIG. 7. The mean percentage of significant intra-guild differences in microhabitat use by assemblage members. Samples were not collected in 1985, 1987, and 1991.

abundant in predator samples and also sometimes occupied deeper microhabitats than smaller *L. coccogenis* (Grossman and Ratajczak 1998). When predators were present, *C. funduloides* occurred closer to shelter over less gravel and sand (Table 5). Differences in the distance from shelter in predator samples may have been affected by seasonal changes in microhabitat availability, because the habitat was deeper in predator samples and the substratum is the main source of shelter for these fishes (Appendix B). In addition, the magnitude of this difference was only 1.4 cm (i.e., predator seasons, mean distance from shelter was 18.8 cm; predator-absent seasons, distance was 20.1 cm), and probably within the range of measurement error for our visual estimation technique. When predators were present, small *O. mykiss* occupied deeper microhabitats farther from the substratum, but closer to shelter, over less sand than when they were absent (Table 5). This result may have been confounded by the fact that we classified large *O. mykiss* as potential predators. Because large *O. mykiss* were present in six of nine predator samples, it is uncertain whether the microhabitat shift exhibited by small *O. mykiss* was a consequence of intraspecific competition with larger conspecifics or a response to predators. The predator-related microhabitat shifts displayed by *N. micropogon* were attributable to either seasonal differences in microhabitat availability or mean length (Table 5, Appendix B). With the exception of *O. mykiss*, water-column guild members did not exhibit predator-related microhabitat shifts that were either strong or readily interpretable as either ecological or behavioral responses to the presence of a predator. In conclusion, results for both benthic and water-column guild members suggest that the presence of potential predators had little effect on the use of spatial resources within this assemblage, and as a consequence, Hypothesis 9 can be rejected.

DISCUSSION

The maintenance of assemblage structure

Ecological assemblages are commonly organized through one of three mechanisms: (1) resource limitation, (2) predation, and (3) environmental variability (Menge and Sutherland 1987). Both descriptive and synthetic aspects of our analysis provided little evidence that two of the three mechanisms (i.e., habitat limitation and predation) had a strong impact on either assemblage structure or the utilization of spatial resources within the Coweeta Creek fish assemblage. This conclusion is based on the following findings. First, changes in assemblage structure, total number of species, and fish microhabitat use and overlap, all coincided with shifts in the hydrologic regime of the site (reject Hypothesis 1, confirm Hypotheses 6–8). Second, we failed to detect a single significant positive correlation between either the total number of species, or number of abundant species and any measure of

habitat availability or microhabitat diversity (reject Hypothesis 2). Third, microhabitat overlap was consistently high and unaffected by factors such as total habitat or microhabitat availability, number of species present, or changes in the abundance of potential competitors (reject Hypotheses 3–5, confirm Hypothesis 8). Only two of 60 comparisons between assemblage characteristics and environmental data yielded significant correlations, and this was less than the number expected by chance alone at either the 0.10 ($N = 6$) or 0.05 level ($N = 3$). One of these results, the significant inverse correlation between the number of species present and total habitat availability, runs contrary to the habitat limitation hypothesis, whereas the other (i.e., the significant inverse correlation between the mean percentage of significant intra-guild differences in microhabitat use and microhabitat diversity) lends some support to this hypothesis. It bears mention, however, that the inverse correlation between microhabitat diversity and microhabitat partitioning was not significant when we compared the mean percentage of significant intra-guild differences in microhabitat use to an alternative measure of microhabitat diversity (i.e., the unpooled standard deviations of seasonal microhabitat availability samples on PCs 1, 2, and 4 of the microhabitat availability analysis).

We also are reluctant to give much credence to the inverse relationship between the percentage of significant intra-guild differences in microhabitat use–microhabitat diversity relationship, because we were unable to detect strong niche shifts by potential competitors in interspecific microhabitat analyses. Consequently, we suggest that it is unlikely that either total habitat or microhabitat limitation had a strong effect on either assemblage structure or the use of spatial resources within the Coweeta Creek fish assemblage. We also suspect that food limitation does not significantly affect the structure of this assemblage, because Stouder (1990) observed a lack of food-resource partitioning during a 19-mo study of this assemblage that encompassed both drought and pre-drought years. Finally, the lack of distinct patterns of assemblage structure or microhabitat use between predator-present and predator-absent samples suggest that this organizational mechanism also does not have a significant impact on this assemblage (reject Hypothesis 9; also see Grossman et al. 1995b).

In contrast to results for resource limitation and predation, environmental variability in the form of variation in flow levels did have a substantial effect on both assemblage structure and microhabitat use in the Coweeta Creek fish assemblage. For example, hydrologic period was the best predictor of assemblage structure in this system (Fig. 4), and the total number of species present was inversely correlated with total habitat availability (mean water-column depth). Variations in the number of species present were attributable to two changes that occurred during the drought: (1) up-

TABLE 4. The effects of potential competitors (second species listed in each pair) on microhabitat use by Coweeta Creek assemblage members (first species listed in each pair).

Species comparison	Samples			Mean length (cm, SL)			Significant components	Variance explained (%)	Variables (loadings in parentheses) for significant components	Significant differences in micro-habitat use	Effect
	R	I	C	R (N)	I (N)	C (N)					
Benthic guild											
<i>C. anomalum</i> vs. <i>H. nigricans</i>	Sp84 A84	A83 Sp88 A89 Sp90 A90	S88	9.1 ^a (55)	9.6 ^a (62)	10.2 ^a (17)	none significant				NS
<i>C. anomalum</i> vs. <i>R. cataractae</i>	Sp90	Sp88 A89	A83 Sp84 A84 S88 A90	8.9 ^a (8)	9.3 ^a (39)	9.6 ^a (87)		10	% cobble (-0.54), % gravel (0.58), % sand (0.55)	C > I	U
<i>R. cataractae</i> vs. <i>C. anomalum</i>	S83 S84 S86 S90 S92		Sp84 A84 Sp88 S88 A89 A90	5.3 ^a (76)	...	4.5 ^b (73)	2	13	% cobble (-0.62), % boulder (0.72), depth (0.51), focal point velocity (0.42)	R > C	L, HA
							4	10	% boulder (-0.48), % bedrock (0.72), % gravel (0.43)	R > C	L, HA
Water-column guild											
<i>C. funduloides</i> vs. <i>L. coccogenis</i>	S83 A83 Sp84 S84 S86 S90	A84 S88 S89 A90 S92 A92	Sp88 A89 Sp90 A90	5.9 ^a (227)	5.4 ^b (125)	5.6 ^b (201)	2	15	% boulder (-0.70), % bedrock (-0.43), % sand (0.60), % cobble (0.54), % gravel (0.52)	R, I > C	L, HA
							3	13	% bedrock (-0.41), distance from substratum (0.75), depth (0.71), distance from shelter (0.44)	C > I, R	L, HA
							4	11	% cobble (-0.64), distance from shelter (0.61), % bedrock (0.47), % sand (0.42)	R, I > C	L, HA
							5	11	% boulder (-0.59), % gravel (-0.40), % bedrock (0.46)	I > R	L, HA
<i>C. funduloides</i> vs. <i>N. micropogon</i>	S83 A83 Sp84 S84 S90 A90 S92 A92	S89 A89 Sp90	S86 Sp88 S88	5.9 ^a (334)	5.3 ^b (103)	5.5 ^b (116)	2	15	% boulder (-0.70), % bedrock (-0.43), % sand (0.60), % cobble (0.54), % gravel (0.52)	C > I	U
							3	13	% bedrock (-0.41), distance from substratum (0.75), depth (0.71), distance from shelter (0.44)	I > R, C	U

TABLE 4. Continued.

Species comparison	Samples			Mean length (cm, SL)			Significant components	Variance explained (%)	Variables (loadings in parentheses) for significant components	Significant differences in micro-habitat use	Effect
	R	I	C	R (N)	I (N)	C (N)					
							5	11	% boulder (-0.59), % gravel (-0.40), % bedrock (0.46)	I, C > R	L, CO
<i>C. funduloides</i> vs. <i>O. mykiss</i>	S83 A83 Sp84	S84 A84 S86 Sp88 S88 Sp90 S90	S89 A89 A90 S92 A92	6.1 ^a (114)	5.7 ^b (285)	5.5 ^b (154)	2	15	% boulder (-0.70), % bedrock (-0.43), % sand (0.60), % cobble (0.54), % gravel (0.52)	I > C	U
							3	13	% bedrock (-0.41), distance from substratum (0.75), depth (0.71), distance from shelter (0.44)	C > I, R	L, HA, CO
							5	11	% boulder (-0.59), % gravel (-0.40), % bedrock (0.46)	I > R	U
<i>C. funduloides</i> vs. <i>S. atromaculatus</i>	A83 Sp84 S84 A84 Sp88 S89 A90 A92	S83 S86 A89 Sp90 S90 S92	S88	5.8 ^a (323)	5.7 ^a (195)	5.2 ^b (35)	5	11	% boulder (-0.59), % gravel (-0.40), % bedrock (0.46)	C > I > R	HA, L, CO
<i>L. cocco-genis</i> vs. <i>N. micropogon</i>	Sp84 A84 S92 A92	A89 A90	Sp88 S88 S89 A89	7.8 ^a (64)	8.7 ^b (38)	7.3 ^a (63)	1	19	% silt (-0.55), % sand (-0.48), focal point velocity (0.82), mean velocity (0.79), distance from substratum (0.41)	I, C > R	HA, L, CO
							2	18	% boulder (-0.76), depth (-0.59), % cobble (0.69), % gravel (0.57)	C > I, R	HA, L, CO
<i>L. cocco-genis</i> vs. <i>S. atromaculatus</i>	Sp84 Sp88	A84 A89 A90 S92	S88 S89 Sp90	6.9 ^a (32)	8.2 ^b (84)	7.9 ^b (39)	2	18	% boulder (-0.70), depth (-0.60), % cobble (0.70), % gravel (0.53)	R > I	U
<i>N. micropogon</i> vs. <i>O. mykiss</i>		S86 Sp88	S88 S89 A89 Sp90 A90	...	7.0 ^a (47)	9.2 ^b (60)	3	11	% gravel (-0.77), % sand (-0.51), depth (0.43)	C > I	U
							4	11	% bedrock (-0.48), distance from substratum (0.71), % sand (0.57)	C > I	U
							5	10	% cobble (-0.46), % bedrock (0.76), distance from substratum (0.44)	C > I	U

TABLE 4. Continued.

Species comparison	Samples			Mean length (cm, SL)			Significant components	Variance explained (%)	Variables (loadings in parentheses) for significant components	Significant differences in microhabitat use	Effect
	R	I	C	R (N)	I (N)	C (N)					
<i>N. micropogon</i> vs. <i>S. atromaculatus</i>	Sp88		S86 S88 S89 Sp90 A90	7.3 ^a (25)	...	8.5 ^b (82)	none significant				NS
<i>O. mykiss</i> vs. <i>L. cocco-genis</i>	S86 S90	S84 S89	Sp84 A84 Sp88 S88 A89 Sp90 A90 S92 A92	9.8 ^{ab} (18)	6.8 ^b (36)	9.8 ^a (162)	none significant				NS
<i>O. mykiss</i> vs. <i>N. micropogon</i>	Sp84 S84 A84 S90 S92 A92	S89 A89 A90	S86 Sp88 S88 Sp90	9.4 ^{ab} (86)	10.7 ^a (70)	7.4 ^b (60)	1	23	% silt (-0.61), % sand (-0.51), % debris (-0.45), mean velocity (0.76), focal point velocity (0.74), depth (0.65)	I > R > C	U
							2	14	% cobble (-0.57), % gravel (-0.50), % boulder (0.61), distance from substratum (0.47)	I > R, C	U
<i>O. mykiss</i> vs. <i>S. atromaculatus</i>	Sp84 S89 A92	S84 Sp88 A89 A90 S92	S86 S88 S88 Sp90 S90	9.7 ^a (40)	9.2 ^a (103)	9.2 ^a (73)	1	23	% silt (-0.61), % sand (-0.51), % debris (-0.45), mean velocity (0.76), focal point velocity (0.74), depth (0.65)	NS	NS
							2	14	% cobble (-0.57), % gravel (-0.50), % boulder (0.61), distance from substratum (0.47)	R, I > C	HA, CO
<i>S. atromaculatus</i> vs. <i>N. micropogon</i>	S83 S84 A84 S90		S86 S88 S89 A89 Sp90	9.4 ^a (30)	...	9.8 ^a (69)	5	10	% gravel (-0.59), % bedrock (0.53), % debris (0.42)	C > R	HA, CO

Notes: Seasons were classified as (1) competitor rare (R, competitor abundance = 0–24% of the abundance of the species being examined), (2) competitor intermediate (I, competitor abundance = 25–49% of the species being examined), or (3) competitor common (C, competitor abundance ≥ 50% of the species being examined). Microhabitat availability analyses tested for significant differences in the microhabitat characteristics of samples when competitor abundances were rare (R), intermediate (I), or common (C) (see Appendix A). Variables that loaded significantly on components but did not differ (univariate data) among treatments by more than our estimated margin of error (i.e., ±2% for substratum data) were not included in our results. We only present data for variables with loadings ≥ 0.401 on components. We also compared the mean lengths of the species being examined during R, I, and C seasons. For both microhabitat availability and length analyses we tested mean scores on significant components using Kruskal-Wallis and Tukey-Kramer a posteriori tests. Samples with the same superscript are not significantly different. Abbreviations for the Effect column are as follows: HA = shifts due to differences in habitat availability between R, I, and C seasons; L = shifts due to differences in mean length of the species examined in R, I, and C seasons coupled with length-specific changes in microhabitat use, CO = interspecific competition, and U = shifts were not interpretable within the context of interspecific competition; NS = not significant. The presence of more than one effect denotes the possibility of multiple causal agents.

TABLE 5. The effects of potential predators on microhabitat use by Coweeta Creek assemblage members.

Species	Mean length (cm, SL)		Component	Variance ex- plained (%)	Variables (loadings in parentheses) for significant components	Signifi- cant differ- ences†	Effect
	P (N)	A (N)					
Benthic guild							
<i>C. anomalum</i>	9.2 ^a (94)	10.1 ^b (40)	4	10	% cobble (-0.54), % gravel (0.58), % sand (0.55)	A > P	HA, L
<i>C. bairdi</i>	5.5 ^a (217)	5.1 ^b (195)	4	11	% boulder (-0.69), % bedrock (0.57), distance from shelter (0.57)	A > P	HA, L
<i>E. blennioides</i>	7.4 ^a (22)	6.3 ^a (13)	none significant				NS
<i>R. cataractae</i>	4.1 ^a (67)	5.5 ^b (82)	1	29	Mean velocity (-0.79), % cobble (-0.59), % gravel (-0.46), % silt (0.86), distance from substratum (0.74), distance from shelter (0.61), % sand (0.51), % debris (0.45)	P > A	HA, L
			2	13	% cobble (-0.62), % boulder (0.72), depth (0.51), focal point velocity (0.42)	A > P	HA, L
Water-column guild							
<i>C. funduloides</i>	5.7 ^a (316)	5.8 ^a (237)	2	15	% boulder (-0.70), % bedrock (-0.43), % sand (0.60), % cobble (0.54), % gravel (0.52)	A > P	HA, Pd
			4	11	% cobble (-0.64), distance from shelter (0.61), % bedrock (0.47), % sand (0.42)	A > P	Pd
			5	11	% boulder (-0.59), % gravel (-0.40), % bedrock (0.46)	P > A	HA, Pd
<i>L. coccogenis</i>	8.0 ^a (121)	7.5 ^a (44)	2	18	% boulder (-0.76), depth (-0.59), % cobble (0.69), % gravel (0.57)	A > P	L, Pd
<i>N. micropogon</i>	8.7 ^a (60)	7.6 ^b (47)	1	19	% silt (-0.63), % debris (-0.55), mean velocity (0.88), focal point velocity (0.46), depth (0.43)	P > A	HA, L
			3	11	% gravel (-0.77), % sand (-0.51), depth (0.43)	P > A	HA, L
<i>O. mykiss</i>	5.3 ^a (55)	5.5 ^a (45)	2	16	% cobble (-0.70), distance from substratum (0.70), % boulder (0.56), depth (0.49)	P > A	HA, Pd
			4	11	% sand (0.48), distance from shelter (0.40)	A > P	HA, Pd

Notes: Samples were classified as either predators absent (A) if predators were not present or predators present (P) if any of the following species were found: *A. rupestris* (≥ 15 cm), *S. atromaculatus* (≥ 15 cm), or *O. mykiss* (≥ 20 cm). Samples with fewer than five prey individuals were deleted from the analysis. We tested for significant predator effects by comparing mean component scores of P and A seasons using Wilcoxon tests. Microhabitat availability analyses tested for significant differences in the microhabitat characteristics of seasons when predators were present and absent (see Appendix B). We also tested for differences in mean lengths between P and A samples using Wilcoxon tests. Values with the same letter were not significantly different. Variables that loaded significantly (i.e., ≥ 10.40) on components but did not differ (univariate data) among treatment groups by more than our estimated margin of error (see Methods) were included in the table but not described in the text. Abbreviations for Effect column were as follows: HA = habitat availability, L = length, and Pd = predator. Multiple abbreviations indicate the possibility of multiple causal factors. Predators were present during S83, A84, Sp88, Su89, A89, Sp90, S90, A90, and A92, and absent in A83, Sp84, S84, S86, S88, and S92. See Methods for further details.

† A86 data were not included in these analyses because we were unable to collect habitat availability data for this sample.

stream migration of species normally resident to lower sections of the creek (i.e., *Lepomis* sp., *M. duquesni*, *N. micropogon*, *N. leuciodus*, and *P. evades*) and (2) downstream emigration by *E. blennioides* (Table 3). Consequently, even though habitat availability decreased significantly during the drought, the study site became habitable for several downstream residents (i.e., *N. micropogon*, *N. leuciodus*, and *P. evades*), and uninhabitable for only one resident species (i.e., *E. blennioides*). There was no evidence, however, that migrants from downstream had a strong impact on mi-

crohabitat use by resident species. In addition, given that many resident species increased in abundance during the drought, it seems unlikely that downstream species had a strong negative impact on residents of the study site. These findings lend further support to our suggestion that habitat was not a limiting resource within the study site, and that assemblage structure was determined primarily by the interaction between flow-induced habitat variation and the behavioral, morphological, and physiological capabilities of assemblage members.

Although migrants from downstream appeared to have little effect on the abundance of resident species or their patterns of microhabitat use, we cannot assume that the converse is true, nor are our data adequate to test for such effects. It is possible that during periods of high or normal flow (e.g., PR or PO), downstream residents were excluded from the study site because residents are superior competitors for trophic or spatial resources. However, occupation of the study site by the two most abundant downstream residents through the PO period, albeit discontinuously (*N. leuciodus*) or at lower abundances (both *N. micropogon* and *N. leuciodus*), suggests that this process either is insufficient to account for the exclusion of downstream species, or is so weak that species can coexist despite competitive interactions for time spans of two to four years. In addition, if competitive interactions between downstream and upstream residents are so weak, why were no migrants observed during PR? These findings lead us to believe that interspecific competition is not the primary factor limiting the upstream distribution of fishes normally resident to downstream areas.

An alternative explanation for the upstream movement of species from downstream is that the distributional limits of these species are set by energetic constraints (Claussen 1936, Li 1975, Brown et al. 1995). Hence, species ascended Coweeta Creek until they reached the point at which a constellation of physical and biological factors (e.g., low temperatures, high velocities, and decreased ability to capture prey) made positive energy balance impossible. Nonetheless, the continued residence of two downstream species in the site despite the resumption of high mean daily flows (i.e., 1989, 1990, and 1992) suggests that the energetic constraint hypothesis also is insufficient to totally account for the patterns observed, unless substantial time lags are involved. Consequently, we are unable to provide a complete explanation for the observed changes in the distribution of downstream residents. For the sake of simplicity, however, we suspect that energetic constraints played a larger causal role in this phenomenon than interspecific competition. In addition, we are currently pursuing studies that will enable us to directly assess the effects of factors such as velocity and temperature on the upstream distribution of several downstream residents in Coweeta Creek.

Besides producing shifts in the distribution of assemblage members, environmental variation also affected the abundance of individual species, although this effect was dependent upon microhabitat guild membership. For example, six of the seven species that increased in abundance during the drought (including migrant species from downstream) belonged to the water-column guilds, whereas only benthic guild members exhibited either unchanged or decreased abundances. Although the drought produced reductions in total habitat availability and mean velocity, as well as small increases in mean water temperature, the most striking

environmental change was the almost cessation of high-flow events $>2.1 \text{ m}^3/\text{s}$ (Fig. 2). The abundances of most species either (water-column guild members) or remained un- (most benthic species) during the drought, it is likely that mortality from high-flow events had a smaller impact on population size during our study than stresses imposed by low flows. This explanation was originally posited by Freeman et al. (1988) who described an inverse relationship between survivorship of both young-of-the-year *C. funduloides* and *O. mykiss* (the two most abundant water-column fishes in Coweeta Creek) and high flows following the reproductive period. In addition, Freeman et al. (1988) also noted the differential effects of high flows on the water-column and benthic members of this assemblage; population sizes of *C. bairdi* and *R. cataractae* (the two most abundant benthic species) were not strongly affected by either high or low flows during their January 1984 through May 1987 study period. Finally, both the differential effects of high flows on the abundance of benthic and water-column species, and the persistence of these disparate responses through high water years (i.e., 1989–1992) argues against the possibility that the observed increases in abundance were an epiphenomenon produced by the concentration of specimens during the drought.

A variety of additional data support the contention that high flows may have substantial negative impacts on fishes in Coweeta Creek. Facey and Grossman (1990, 1992) have shown that high velocities have a greater effect on the ecological performance (e.g., energy expenditure and microhabitat use) of *C. funduloides* and *O. mykiss* than on *C. bairdi* and *R. cataractae*. Hill and Grossman (1987) also documented that high flows were capable of displacing *C. funduloides* high flows were capable of displacing *C. funduloides* downstream out of their home ranges, whereas high flows had little effect on the movements of *C. bairdi* or *R. cataractae*. In addition, Hill and Grossman (1993) demonstrated that the decrease in foraging success experienced by *C. funduloides* and *O. mykiss* at high velocities was the primary factor affecting optimal microhabitat choice in these species. Hence, counter to our initial expectation that the drought would have a significant negative effect on assemblage members, it appears to have facilitated survivorship in many water-column species, probably via a reduction in the deleterious impacts of high flows (i.e., increased mortality, decreased foraging success, increased energetic costs, etc.).

Variability in flows has been shown to affect the structure of many stream fish assemblages (Starrett 1951, Larimore et al. 1959, Deacon 1961, Horowitz 1978, Schlosser 1985, Erman et al. 1988, Schlosser and Ebel 1989, Pusey et al. 1993, Poff and Allan 1995) primarily through its effect on mortality and subsequent recruitment. In fact, several authors have suggested that the unpredictable nature of floods and droughts coupled

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with their strong potential impacts on the stream biota may play a dominant role in the organization of stream fish assemblages (Horowitz 1978, Grossman et al. 1982, Poff and Allan 1995). Subsequent research has identified streams in which hydrologic variability has a great influence on the ecological characteristics of fish assemblages (Fausch and Bramblett 1991, Strange et al. 1992, Poff and Allen 1995), whereas others have concluded that this process has little impact (Meffe and Minckley 1987, Matthews et al. 1988, Meffe and Berra 1988). Schlosser (1987) suggested that stream fish assemblages in the Midwestern United States are organized via a regulatory continuum. Environmental unpredictability plays a dominant role in headwater streams, whereas competition and predation are more important downstream. Schlosser and Ebel (1989) provided evidence to support this prediction; however, other studies demonstrate that environmental variability can have a substantial impact on the structure of stream fish assemblages in larger streams (Capone and Kushlan 1991, Fausch and Bramblett 1991), even in the Midwestern United States (Grossman et al. 1982, Grossman et al. 1990, Poff and Allen 1995).

It is common for researchers to fail to detect relationships between fish species diversity or total number of species present and microhabitat availability or diversity in streams (Angermeier and Schlosser 1989, Bart 1989). Grossman et al. (1982), Schlosser (1982), and Angermeier and Schlosser (1989) all suggest that the presence of such relationships is unlikely if environmental variability reduces stream fish populations to levels below which resource limitation occurs. Nonetheless, other researchers have identified streams in which habitat availability/diversity is a good predictor of: (1) the number of fish species present, (2) fish species diversity, or (3) assemblage composition (Gorman and Karr 1978, Angermeier and Karr 1984, Meffe and Sheldon 1988, Angermeier and Schlosser 1989, and Pusey et al. 1993, 1995). It is possible that these discrepancies are due to differences in the relative physicochemical stability of the systems examined.

Microhabitat use and overlap

Despite reasonably high species diversity, stream fish assemblages in the Northern Hemisphere typically are dominated by members of a few families (e.g., Cyprinidae, Percidae, Cottidae, Salmonidae, and Catostomidae). For example, we observed a total of 16 species in Coweeta Creek all of which were members of the aforementioned families. Despite the common evolutionary history of taxonomically similar species, and the increased likelihood of interspecific competition, the members of many stream fish assemblages exhibit a lack of strong differentiation in microhabitat use (Matthews and Hill 1980, Grossman and Freeman 1987, McNeeley 1987, Ross et al. 1987, Bain et al. 1988, Meffe and Sheldon 1988, Bart 1989, Grossman and de Sostoa 1994a, b, Brown et al. 1995). Nonethe-

less, other investigators have demonstrated that stream fishes segregate along a variety of axes including substratum type (Finger 1982, Daniels 1987, Baltz and Moyle 1993) and position in the water column (Baker and Ross 1981, Gorman 1988a, b, Baltz and Moyle 1993), although Baltz and Moyle (1993) have shown that such segregation is not necessarily a result of interspecific competition. Our data indicate that species could be classified as members of one of three microhabitat guilds: (1) benthic, (2) lower water column, and (3) mid-water column. Species generally retained membership in a single guild, and typically were not statistically differentiable from members of the same guild. In contrast, members of different guilds generally were statistically separable, although this was not always true for members of the lower-water-column guild. The maintenance of high overlap in microhabitat use over ecologically significant time scales (i.e., 10 yr) suggests that interspecific competition plays a limited role in determining microhabitat use within this assemblage. In fact, because of the many covarying environmental factors influencing any field study, we also have examined the interaction between interspecific competition and microhabitat use by the four most abundant species in this assemblage experimentally (i.e., benthic guild members, *C. bairdi* and *R. cataractae*; mid-water-column guild members, *C. funduloides*, and *O. mykiss*). All of these studies failed to find a significant interspecific effect on the use of spatial resources by the remaining member of the species pair (effect of *R. cataractae* on *C. bairdi*, Barrett 1989; effect of *C. bairdi* on *R. cataractae*, Stouder 1990; effect of *C. funduloides* on *O. mykiss*, Grossman and Boule 1991; effect of *O. mykiss* on *C. funduloides*, Rincon and Grossman 1998). In addition, neither Barrett (1989) nor Stouder (1990) found that interspecific competition produced shifts in the use of trophic resources by either *C. bairdi* (vs. *R. cataractae*) or *R. cataractae* (vs. *C. bairdi*); in both cases intraspecific interactions were much stronger than interspecific effects. These findings support our conclusion that interspecific competition has little impact on the use of spatial resources by members of the Coweeta Creek fish assemblage.

CONCLUSION

Coweeta Creek exhibits a level of variability in flows similar to that of many streams in North America (Poff and Ward 1989). Our data show that environmental variability manifested through variations in flow had a much stronger impact on both assemblage structure and patterns of microhabitat use and overlap than either habitat limitation or predation. Consequently, we suggest that the ecological patterns observed in this assemblage are a product of the interaction between environmental variation and species-specific evolutionary constraints on behavior, morphology, and physiology. It is likely that long-term descriptive studies,

coupled with both field and laboratory experiments, will be required to identify the major organizational processes operating in other animal assemblages. The need for such studies has been exacerbated by the potential impacts of large-scale ecological perturbations such as landscape changes, global warming, and depletion of the ozone layer.

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APPENDIX A

PCA test for significant differences in microhabitat availability data for samples when potential competitors (the second species listed in each pair) were present at different levels of abundance.

Species comparison	Component number	Variance explained (%)	Variables (loadings in parentheses) for significant components	Significant differences in microhabitat availability
Benthic guild				
<i>C. anomalum</i> vs. <i>R. cataractae</i>	none significant			
<i>R. cataractae</i> vs. <i>C. anomalum</i>	1	25	% silt (–0.75), % debris (–0.52), % sand (–0.48), mean velocity (0.83), % cobble (0.49)	C > R
	4	12	% boulder (–0.49), depth (0.64), % debris (0.41)	C > R
Water-column guild				
<i>C. funduloides</i> vs. <i>L. cocconeus</i>	1	25	% silt (–0.71), % debris (–0.53), % sand (–0.44), mean velocity (0.85), % cobble (0.51), % gravel (0.41)	C > R, I
	4	12	% boulder (–0.51), depth (0.44)	C > R
<i>C. funduloides</i> vs. <i>N. microgobius</i>	1	25	% silt (–0.71), % debris (–0.53), % sand (–0.44), mean velocity (0.85), % cobble (0.51), % gravel (0.41)	I > R > C
	2	18	% cobble (–0.63), % gravel (–0.56), % bedrock (0.60), % boulder (0.58)	R, I > C

APPENDIX A. Continued.

Species comparison	Component number	Variance explained (%)	Variables (loadings in parentheses) for significant components	Significant differences in microhabitat availability
<i>C. funduloides</i> vs. <i>O. mykiss</i>	1	25	% silt (-0.71), % debris (-0.53), % sand (-0.44), mean velocity (0.85), % cobble (0.51), % gravel (0.41)	C > I
	2	18	% cobble (-0.63), % gravel (-0.56), % bedrock (0.60), % boulder (0.58)	C > I
	4	12	% boulder (-0.51), depth (0.44)	C > I
<i>C. funduloides</i> vs. <i>S. atromaculatus</i>	2	18	% cobble (-0.63), % gravel (-0.56), % bedrock (0.60), % boulder (0.58)	R, I > C
<i>L. coccogenis</i> vs. <i>N. micropogon</i>	1	25	% silt (-0.71), % debris (-0.54), % sand (-0.42), mean velocity (0.85), % cobble (0.50)	I > C
<i>L. coccogenis</i> vs. <i>S. atromaculatus</i>	4	11	% sand (0.68), depth (0.58)	R > C
<i>N. micropogon</i> vs. <i>O. mykiss</i>	1	25	% silt (-0.72), % debris (-0.48), % sand (-0.47), mean velocity (0.83), % cobble (0.60), % gravel (0.40)	C > I
	2	18	% gravel (-0.54), % cobble (-0.51), % boulder (0.71), % bedrock (0.74)	C > I
	4	13	% boulder (-0.47), depth (0.76)	I > R, C
<i>O. mykiss</i> vs. <i>N. micropogon</i>	1	25	% silt (-0.72), % debris (-0.52), % sand (-0.41), mean velocity (0.84), % cobble (0.54), % gravel (0.41)	I > R, C
	2	18	% cobble (-0.59), % gravel (-0.56), % boulder (0.65), % bedrock (0.51)	R, I > C
	4	12	% boulder (-0.52), depth (0.59)	I > C
	5	11	% sand (0.82), depth (0.43)	R > C
<i>O. mykiss</i> vs. <i>S. atromaculatus</i>	1	25	% silt (-0.72), % debris (-0.52), % sand (-0.41), mean velocity (0.84), % cobble (0.54), % gravel (0.41)	R, I > C
	4	12	% boulder (-0.52), depth (0.59)	I > C
<i>S. atromaculatus</i> vs. <i>N. micropogon</i>	1	24	% silt (-0.72), % debris (-0.51), % sand (-0.45), mean velocity (0.85), % cobble (0.43)	C > R

Notes: Seasons were classified as: (1) competitor rare (R), competitor abundance = 0-24% of the abundance of the species being examined, (2) competitor intermediate (I), competitor abundance = 25-50% of the species being examined, or (3) competitor common (C), competitor abundance > 50% of the species being examined. We tested for significant differences in mean component scores for different competitor abundance classes using Kruskal-Wallis tests followed by Tukey-Kramer a posteriori tests. We only present data for variables that had loadings $\geq |0.40|$ on components. See *Methods* for further details.

APPENDIX B

PCA test for significant differences in microhabitat availability data between samples where potential predators were present (P) or absent (A).

Species	Component number	Variance explained (%)	Variables (loadings in parentheses) for significant components	Significant differences
Benthic guild				
<i>C. anomalum</i>	none significant			
<i>C. bairdi</i>	2	18	% cobble (-0.63), % gravel (-0.56), % bedrock (0.60), % boulder (0.58)	P > A
	4	12	% boulder (-0.51), depth (0.44)	P > A
<i>E. blennioides</i>	2	20	% boulder (-0.60), % bedrock (-0.57), % gravel (0.62), % cobble (0.59), % sand (0.46)	A > P
	3	14	% boulder (-0.71), depth (0.67), % bedrock (0.55)	P > A
<i>R. cataractae</i>	2	18	% cobble (-0.66), % gravel (-0.55), % bedrock (0.62), % boulder (0.58)	P > A
	4	12	% boulder (-0.49), depth (0.64), % debris (0.41)	P > A
Water-column guild				
<i>C. funduloides</i>	2	18	% cobble (-0.63), % gravel (-0.56), % bedrock (0.60), % boulder (0.58)	P > A
	4	12	% boulder (0.51), depth (0.44)	P > A
<i>L. coccogenis</i>	none significant			
<i>N. micropogon</i>	1	25	% silt (-0.72), % debris (-0.48), % sand (-0.47), mean velocity (0.83), % cobble (0.60), % gravel (0.40)	P > A
	2	18	% gravel (-0.54), % cobble (-0.51), % boulder (0.71), % bedrock (0.47)	P > A
	4	13	% boulder (-0.47), depth (0.76)	P > A
<i>O. mykiss</i>	2	17	% cobble (-0.62), % gravel (0.55), % bedrock (0.65), % boulder (0.49)	P > A

Notes: We tested for significant differences in mean component scores between predator abundance classes using Wilcoxon tests. We only present data for variables with loadings $\geq |0.40|$ on components. See *Methods* for further details.